ONTOGENY OF THERMOREGULATION IN RED-TAILED HAWKS AND SWAINSON'S HAWKS

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ABSTRACT.—Nestling Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks, (*B. swainsoni*), exposed daily to ambient temperatures of 5 and 16°C, showed gradual thermoregulatory improvements that most closely correlated with nestling age, the log of nestling age, or the log of nestling mass. Although thermal stability improved with increasing body size, the near normal thermoregulatory development of runt nestlings indicates that endothermy is primarily attained through factors other than body size. When nestlings were exposed to a radiation load of 1 cal/cm²/min and rising ambient temperatures, their abilities to control rising body temperature were not highly correlated with age or four other growth parameters. In the wild, hyperthermia is probably a greater threat to these cold-hardy nestlings than is hypothermia. *Received 20 Jan. 1989, accepted 15 April 1989.*

The pattern of transition from ectothermy to endothermy among nestling birds shows much interspecific variability (O'Connor 1984). Thermal extremes encountered by nestlings of many species may be a major obstacle to nestling survival.

The ontogeny of thermoregulation in nestling diurnal birds of prey is poorly known in spite of the relative abundance of information on raptor breeding biology (Newton 1979). In this study our objective was to determine the patterns of endothermic development in young Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks (*B. swainsoni*). In northern Utah, the nestling periods of Red-tailed Hawks (RT) normally span approximately 10 weeks from the earliest hatchings in late April to the latest fledglings in early July. Nestlings are sometimes exposed to relatively cool conditions (e.g., air temperatures near freezing, high winds, and rainstorms) during this period when they are dependent on the adults for food and thermal protection. The nestling period of the Swainson's Hawk (SW) is about one month later in northern Utah with earliest hatchings in early June and latest fledgings in mid August. During these nestling periods young hawks in unshaded nests can face the thermoregulatory challenge of heat stress caused by intense, direct solar radiation and air temperatures above 30°C.

METHODS

The hawk nestlings investigated during this study (6 RT and 10 SW) werc obtained from nests in 1979 in northern Utah (Cache Valley, elev. 1340 to 1524 m).

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TABLE 1

ENVIRONMENTAL CONDITIONS DURING TESTS OF NESTLING THERMOREGULATORY ABILITY.
AMBIENT TEMPERATURE INCREASED DURING TEST 3 FROM THE INITIAL TEMPERATURE (I)
TO THE FINAL TEMPERATURE (F)

		Test conditions		
		Ambient temperature (°C)	Duration (min)	Artificial radiation (cal/cm²/min)
Test 1				
Red-tailed Hawk		16.2	30	trace
Swainson's Hawk		15.7	30	trace
Test 2				
Red-tailed Hawk		5.4	30	trace
Swainson's Hawk		5.5	30	trace
Test 3				
Red-tailed Hawk	I	12.7	20	1
	F	22.7		
Swainson's Hawk	I	12.1	20	1
	F	23.9		

Testing of thermoregulatory performance.—Nestlings were randomly selected in pairs from nests containing three young estimated to be less than one week old (except in the case of two RT nestlings estimated to be 12 and 8 days old). Ages of the nestlings were estimated from their body weights during the first 24 h of captivity by comparing with weights of wild, known-age young. Nestlings were kept on an artificial nest (70 cm × 100 cm) of sticks and shredded bark within a walk-in environmental chamber. A carpeted stove pipe, heated to a stable surface temperature of 38°C by light bulbs mounted inside, was accessible to the nestlings for heat.

Air temperature within the environmental chamber was maintained at 16 ± 2°C, except during the thermoregulatory tests described below. Humidity within the chamber was not controlled or monitored and photoperiod was similar to that occurring naturally in northern Utah during May and June (i.e., 15 h light : 9 h dark), except that it was shifted 2 h later than normal. The nestling food was a mixture of domestic hamsters and black-tailed jack-rabbits (*Lepus californicus*); the head, stomach, and intestines were removed before grinding in a Waring blender.

Prior to the first feeding each morning, we measured four growth parameters on each nestling. Body weight was measured to the nearest 0.1 g with an Ohaus triple beam balance. Length of the tarsus and of the seventh primary feather was measured to the nearest 0.1 mm with a dial caliper in the standard manner (Baldwin et al. 1931). Thickness of the downy plumage along the dorsal midline between the bases of the wings was measured with a dial caliper to the nearest 0.1 mm.

Thermoregulatory performance of the nestlings was tested daily by exposing them to three sets of conditions (Table 1) which simulated thermal environments encountered by raptors nesting in northern Utah. Tests 1 and 2 were designed to determine nestling endothermic capabilities at moderately cool (16 ± 2°C) and cold (5 ± 1°C) air temperatures (T_a), re-

spectively. Irradiance was negligible in the dimly lighted chamber during Tests 1 and 2. Test 3 simulated the thermal conditions at unshaded nests exposed to direct solar radiation and a moderate range of air temperatures (12–24°C). Chamber air was circulated with a room fan, but air flow was not directed at the nestlings. The radiation source for Test 3 was a reflective panel of twelve 300 watt unfrosted, incandescent light bulbs which produced 1.0 to 1.2 cal/cm²/min (as measured with a Schenk Star pyranometer) over the entire nest surface. During Test 3 the heat produced by the lights exceeded the cooling capacity of the chamber and air temperature during the 20-min test period rose approximately 11–12°C (e.g., from 12 to 24°C).

On days when two tests were performed in succession, at least 1 h was allowed for re-establishment of normal nestling body temperatures before the start of the next test. During each test run all nestlings were exposed and monitored simultaneously. During Tests 1 and 2, plastic mesh dividers prevented nestlings from huddling together. During Test 3, nestlings were permitted unrestricted movement about the nest surface. At 5-min intervals throughout the test periods, temperatures of ambient air and nestlings were measured to the nearest 0.1°C with copper-constantan thermocouples (24 ga) and a calibrated thermocouple thermometer (model TH 50, Wescor Inc., Logan, Utah). Thermocouple probes (one shielded, one unshielded) were located on the nest margin. We monitored the body temperature of each nestling with an epoxy-coated thermocouple inserted 2.5 cm through the cloaca and held in this position by a harness of plastic and leather strips (Fig. 1).

Two measures of thermoregulatory performance were calculated from the body temperature records of each nestling during each trial: (1) absolute change in nestling body temperature during the test period (ΔT_b in °C) and (2) the rate of body temperature change (i.e., slope of the least squares regression of T_b versus time, expressed as °C/min).

Age, growth, and thermoregulatory performance data were analyzed with a stepwise multiple regression to determine the measures of age and growth most correlated with the two measures of nestling thermoregulatory performance. Transformations of the five independent variables (i.e., age, body weight, tarsal length, plumage depth, and the length of the seventh primary feather) were used within a quadratic and a log model. The data for each of the three thermoregulatory tests were analyzed separately. Within each test, data from each of the two species were analyzed independently.

We measured body temperature changes in five dead nestlings (ranging in weight from 42 to 323 g) exposed to the three test conditions to assess the importance of body size and plumage on nestling thermoregulatory performance. Nestling carcasses were kept fresh by refrigeration and were tested only if they showed little dehydration (reduction in weight) or plumage alteration. Prior to each test, the body temperature of each nestling carcass was raised to a normal level (38–40°C) by placing the carcass in a warm drying oven, and then the carcass was exposed to the same three test conditions for the same lengths of time as described for live birds.

Respiration rates of randomly selected nestlings were recorded during some of the trials of Tests 1 and 3 with an impedance pneumograph and a Physiograph (E & M Instrument Co.).

RESULTS

Test 1.—The youngest nestlings of both hawk species cooled at similar rates when exposed to 16 ± 2°C. Declines in T_b were correlated with nestling age (Fig. 2). Body temperature of nestlings older than 10 to 12 days rarely decreased more than 1°C, and in some cases, nestlings older than 11 days had final body temperatures a few tenths of a degree higher

leather thong

plastic cable tie

cloacal probe

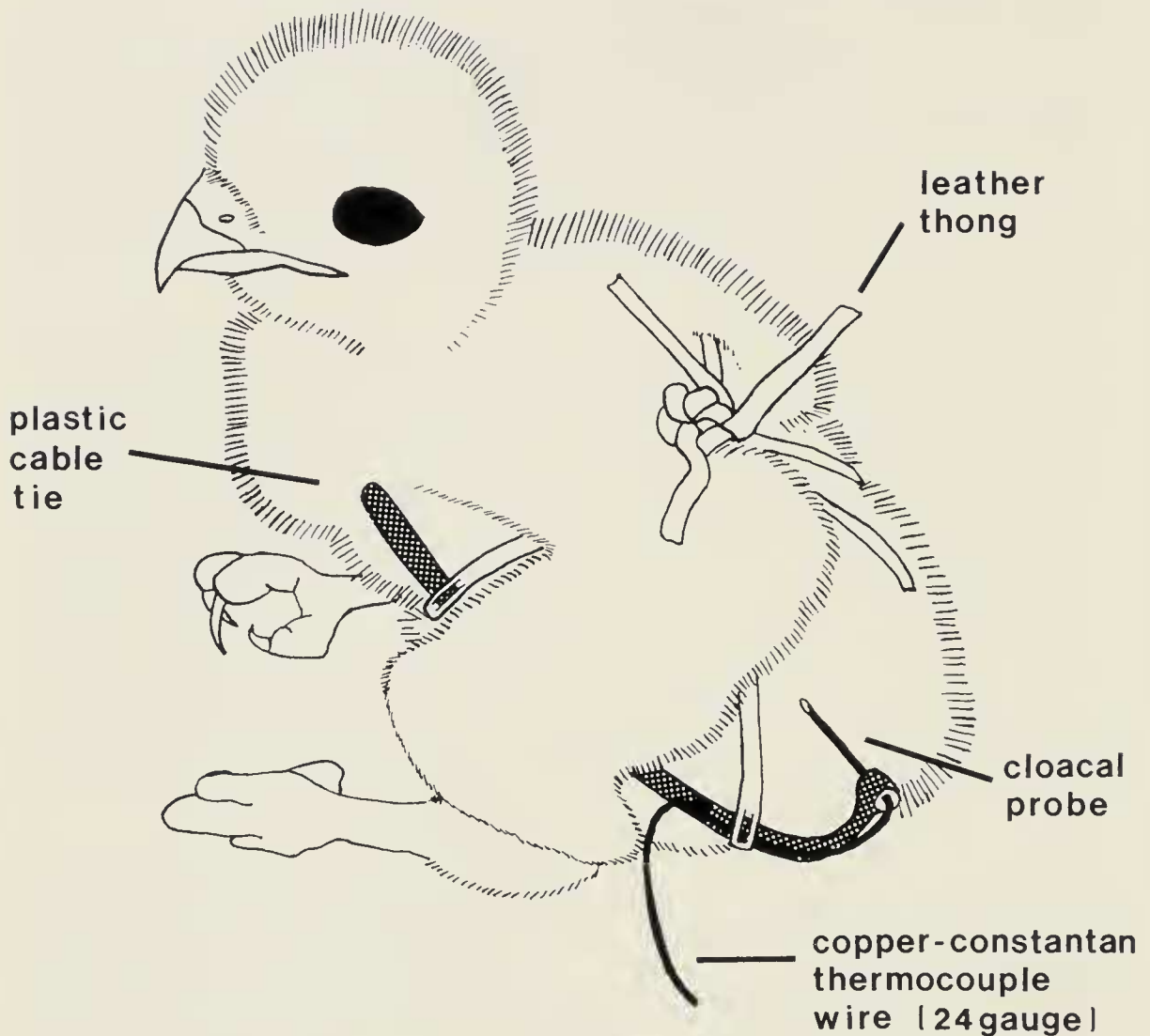**copper-constantan thermocouple wire (24 gauge)**

FIG. 1. Harness designed to hold thermocouple in the cloaca.

than their initial body temperatures. Age and log age were the best predictors of thermoregulatory performance for both species (Table 2). Body temperatures of the slowest growing nestling of each species frequently decreased to slightly lower levels than those of conspecifics of the same age, due, in part, to the lower pretest T_b of these runts.

Test 2. —As expected, nestling body temperatures fell more rapidly in Test 2 than in Test 1 (Fig. 2). Rate of cooling and ΔT_b were related to nestling age as in Test 1. Body temperature declines rarely exceeded 1°C in nestlings older than 13 to 15 days, and in a few instances, the body temperature of older nestlings increased over the test period. Once again, the slowest growing nestlings had slightly retarded body temperature control compared to nestlings with normal growth rates. Nestling age accounted for the highest proportion of the variability in the two dependent variables in both species when the independent variables were either
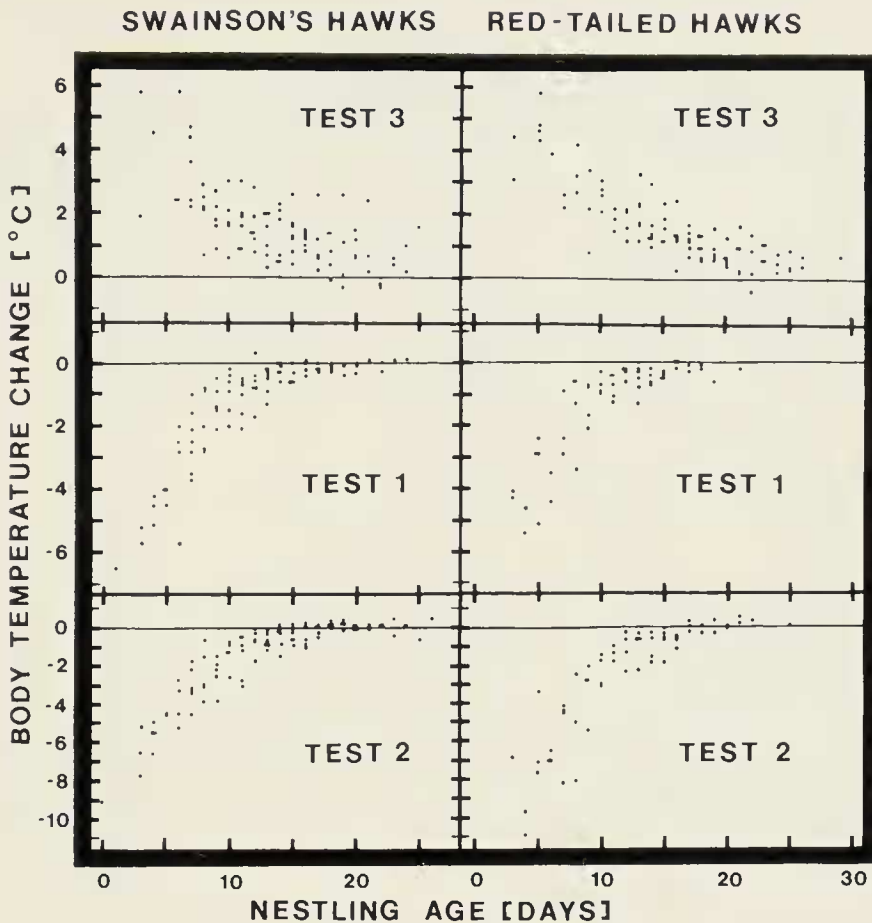
FIG. 2. Body temperature change versus age of Red-tailed Hawk and Swainson's Hawk nestlings exposed to: $T_a = 16°C$ for 30 min (Test 1), $T_a = 5°C$ for 30 min (Test 2), and $T_a = 12$ to $23°C$ and short wave radiation $= 1$ cal/cm²/min for 20 min (Test 3).

untransformed or quadratically transformed (Table 2). When log-transformed variables were analyzed in Red-tailed Hawks, log age was the most important independent variable, whereas log body weight was the most important independent variable in Swainson's Hawks.

Heat retention improved with increasing body size of dead nestlings (Table 3). However, the body temperature decline of the largest carcass (323 g, which is a typical mass for 11–13-day-old nestlings) was about the same as that of live nestlings at 3 to 5 days of age; therefore, the improvement in nestling thermoregulation involves more than simply greater heat retention from improved feather insulation or greater body mass.

Qualitative observations of nestlings during the low temperature tests suggested that the youngest nestlings were more active in the cold than older nestlings; they struggled and vocalized as if uncomfortable or distressed. In contrast, the older nestlings lay quietly with wings and legs held close to the body and shivered visibly.

TABLE 2
SUMMARY OF THE MULTIPLE REGRESSION ANALYSES

Thermoreg. test analyzed	Model	Species[a]	Single most important independent variable[b]	Proportion of variability accounted for in the dependent variable (R^2)	
				T_b	Slope ΔT_b/time
Test 1	Quad	RT	Age	0.64	0.61
	Quad	SW	Age	0.64	0.62
	Log	RT	Log age	0.75	0.73
	Log	SW	Log age	0.80	0.78
Test 2	Quad	RT	Age	0.69	0.69
	Quad	SW	Age	0.68	0.69
	Log	RT	Log age	0.79	0.80
	Log	SW	Log body weight	0.84	0.83
Test 3	Quad	RT	Age	0.68	0.66
	Quad	SW	Tarsal length	0.39	0.34
	Log	RT	Log age	0.73	0.75
	Log	SW	Log plumage depth	0.43	0.38

[a] RT = Red-tailed hawk, SW = Swainson's hawk.
[b] Five independent variables were used; age, body weight, tarsal length, plumage depth, and length of the seventh primary feather.

For each species, respiratory frequencies at the beginning of Tests 1 and 3 and at the end of Test 1 (Table 4) were not significantly different (F-test, $P > 0.05$). Swainson's Hawk nestlings had a significantly higher average breathing rate (49.3/min) than did Red-tailed Hawks (36.4/min; t-test, $P < 0.001$).

Test 3. — The body temperatures of nestlings exposed to the irradiance and moderate temperatures of Test 3 usually increased gradually, but the final body temperature rarely exceeded 42°C. The maximum body temperature of Red-tailed Hawks was 42.3°C and of Swainson's Hawks 42.8°C (this nestling died immediately after that trial). In general, the increases in nestling body temperature rarely exceeded 3°C except for young nestlings with low initial temperatures. In a few instances the body temperatures of older nestlings decreased over the test period (Fig. 2). The apparent improvement in thermoregulatory control with age is somewhat exaggerated by the graphs for Test 3 because the initial body temperatures of young nestlings were generally a few degrees lower than those of older nestlings. Thus, some young nestlings had body temperature increases of 4 to 6°C but they did not become excessively hyperthermic (Fig. 2).

For Red-tailed Hawks age accounted for 68 and 66% of the variability in the dependent variables, ΔT_b and slope ΔT_b/time, respectively; log age

TABLE 3

SUMMARY OF BODY TEMPERATURE CHANGES OF THE CARCASSES OF RED-TAILED AND
SWAINSON'S HAWK NESTLINGS EXPOSED TO THREE ENVIRONMENTAL TEST CONDITIONS
(TABLE 1 DESCRIBES THE ENVIRONMENTAL CONDITIONS OF THESE TESTS)

Nestling carcasses			Average body temperature change (°C)		
Body weight (g)	Equivalent age (days)	Number of carcasses	Test 1 (N)	Test 2 (N)	Test 3 (N)
42–45	0–2	2	−11.5 (3)	−13.0 (2)	+4.4 (4)
109–120	4–6	2	−7.3 (2)	−9.9 (3)	+5.6 (3)
323	11–13	1	−7.1 (2)	−7.2 (1)	+0.7 (2)

accounted for 73 and 75% of the variability, respectively. Body temper-
ature change and rate of body heating in Swainson's Hawks were best
correlated with tarsal length and log plumage thickness, though individ-
ually, these variables accounted only for 34 to 43% of the variation in
the dependent variables (Table 2). The thermoregulatory performance of
individual nestlings varied from one day to the next in Test 3, thus
precluding a high level of predictability using any of the independent
variables. Less precise control of the ambient temperature in Test 3 re-
sulted in greater variability in the test conditions which may also account
for some of the inconsistency in nestling thermoregulatory performances.
Body temperature increases within the two smallest size classes of nestling
carcasses were similar to those of live nestlings of similar size, but the
temperature increase of the largest carcass was less than that of live nest-
lings of the same size (Table 3).

One Swainson's Hawk died within minutes of the conclusion of Test
3, as mentioned previously, when its maximum body temperature had
reached 42.8°C. During the same trial, the maximum body temperatures
of two other Swainson's Hawks which later died were 42.6 and 41.1°C.
Although neither of the latter two nestlings was subsequently exposed to
the conditions of Test 3, both regurgitated food, lost weight, and died
three to four days later. It is unlikely that the brief elevation of T_b of these
three nestlings was the primary cause of their death. Dehydration may
have been a factor in the deaths of these birds; their carcasses were about
10% lower in body water than carcasses of wild nestlings.

Regardless of age, the behavior of all nestlings during Test 3 was similar
in many respects. Nestlings tended to move out from the nest center to
the perimeter, their breathing rates increased, they assumed body postures
characteristic of heat-stressed birds, and they showed signs of discomfort.
Nestlings of all ages struggled out onto the loose sticks of the nest edge,

TABLE 4

RESPIRATION RATES OF NESTLINGS DURING THERMOREGULATORY TESTS 1 AND 3 AS DETERMINED BY AN IMPEDANCE PNEUMOGRAPH. (SEE TABLE 1 FOR ENVIRONMENTAL CONDITIONS DURING THESE TESTS)

Species	Test	Average respiration rate (breaths per minute)	
		Initial (N)	Final (N)
Red-tailed Hawk	1	34.9 (15)	36.5 (15)
	3	37.0 (38)	176.6 (35)
Swainson's Hawk	1	46.1 (11)	48.4 (9)
	3	54.1 (9)	164.9 (9)

often selecting the same side of the nest; the direction of circulating room air may have caused a greater air flow at that location.

The time of onset of panting varied considerably. The youngest nestlings began to pant after four to six minutes of exposure, while some of the oldest nestlings panted only when exposure extended beyond the normal 20 min. Average respiration rates increased significantly (F-test, $P < 0.05$) from 37 and 54 breaths per min to 177 and 165 per minute in Red-tailed and Swainson's hawks, respectively (Table 4). Final breathing rates of these two species did not differ significantly. The maximum breathing rates we measured in Red-tailed and Swainson's hawks were 264 and 192 per min, respectively.

The typical body posture of heat stressed nestlings includes an alert, upright sitting posture with the wings either spread or loosely drooped to the sides, and with the legs held forward exposing the feet and tarsi. Nestling discomfort was suggested by high, sharp vocalizations, and frequent nervous shifting of positions on the nest. After the light panel was turned off following each trial, nestlings continued to pant for 3 to 7 min, and their body temperatures returned to normal in approximately 15 to 20 min.

DISCUSSION

Growth.—Growth rates of the captive nestlings were similar to those of the wild-reared nestlings we measured and to those of Red-tailed and Swainson's hawk nestlings studied by others (Olendorff 1971, Ricklefs 1968, Parker 1976). Some of our captive-reared nestlings grew more slowly than their conspecifics, a condition which, in wild-reared nestlings, is generally assumed to result from an unequal distribution of food to the nestlings. In contrast, all the captive nestlings were fed at frequent intervals

until satiated to insure adequate nourishment; therefore, the cause of slow growing individuals among the captive-reared nestlings is unclear. Thermoregulatory development of runt nestlings was only slightly retarded despite their slow physical growth, at times 30–50% lower than the weight of normal nestlings.

During the first 10 days of growth, nestling thermoregulation under cold conditions improved markedly (Fig. 2), but, of the four growth variables we measured, only body weight and tarsal length underwent much change. The feathers of the alar tract are practically nonexistent during this period, the first small eruptions beginning at 8–12 days of age. Before day 10, the thickness of the downy plumage remains relatively constant, and secondary down has just begun to replace primary down. This suggests to us that little, if any, of the early thermoregulatory development is due to improved insulation from the plumage.

The decrease of surface to volume ratio and increase of thermal mass during nestling growth provide greater thermal stability. Predictably, the tests on nestling carcasses showed that a larger body mass cooled less quickly in the cold and warmed more slowly under a radiation load than did a smaller body mass. However, body size cannot entirely account for the development of thermoregulation in these two hawk species since thermoregulatory development was not significantly retarded in undersized runt nestlings. Presumably, some physiological change is primarily responsible for the transition to endothermy in these hawk nestlings as suggested by O'Connor (1984).

Tolerance to hypothermia.—The responses of avian young to cold vary considerably. Nestlings of some species withstand long periods of exposure to cold, their bodies chill (T_b = 15–20°C) until they cannot move, yet when rewarmed they have no detectable adverse effects (O'Connor 1984, Dawson and Evans 1957; 1960; Dawson et al. 1972; Howell 1964). Some precocial young, although better thermoregulators than altricial young at hatching, are less tolerant to chilling at an early age; brief exposures (30 min) to moderate temperatures (20°C) can impair thermoregulatory development or cause death (Bernstein 1973, Ryser and Morrison 1954).

Red-tailed and Swainson's hawk nestlings are similar to the more cold-hardy avian species; they tolerated repeated daily exposures to the cold conditions of Tests 1 and 2. Cold-hardiness in Red-tailed Hawk nestlings was also recorded at three nests (abandoned by parental birds after placement of time-lapse cameras), where four of six nestlings survived one night of exposure, two nestlings survived two nights of exposure, and one nestling survived three nights of exposure (Kirkley 1982). Differential survival times may have been due to differences in nestling energy reserves or differences in the thermal conditions at each nest, causing different

rates of energy depletion. In hawk nests with normal parental attentiveness, nestling mortality from hypothermia is probably not a common cause of mortality, unless severe hypothermia occurs from rapid heat losses following wetting of the plumage or during strong, cold winds (Hodson 1975).

Age of endothermy. — The thermoregulatory ability of recently hatched Red-tailed and Swainson's hawk nestlings appears to be about in the middle of the graded series of thermoregulatory abilities of bird species discussed by O'Connor (1984). For instance, the 3–4°C decline in body temperature of youngest hawks after 10 min of cold exposure is comparable to the thermoregulatory abilities of some typical gallinaceous species; it is poorer than that of the precocial young of ducks but is much better than that of the altricial young of pigeons and passerines.

Dunn (1975) defined the age of endothermy in altricial birds as "that age at which nestlings can keep their body temperatures at least 75% as high above an ambient temperature of 20°C as can an adult, after some period of exposure" and she later specifies the period of exposure as "at least 20 minutes" (Dunn 1976). The nestlings we exposed to 16°C (Test 1) were endothermic at 4–5 days of age by Dunn's criteria (assuming that the body temperature of an adult hawk is 41°C). Caution should be used in applying Dunn's arbitrary definition of endothermy, however, because even our largest dead nestling (325 g) would marginally qualify as endothermic under Dunn's criteria. Dunn (1975) also indicated that the age of endothermy in 22 altricial species (adult weights ranged from 10.8 to 2050.0 g) is most highly correlated with their growth constants (K). We note that our hawk nestlings, classified as semi-altricial young, do not fit the relationship found for altricials. For example, Red-tailed and Swainson's hawk nestlings attained Dunn's age of endothermy eight to nine days earlier than would be predicted for a similarly growing altricial nestling (assuming K values of 0.161 to 0.202 as reported by Olendorff 1971 and Parker 1976).

Although Dunn's definition of the age of endothermy facilitates interspecific comparisons, its biological significance is ambiguous. Gradual and progressive endothermic development makes selecting an endpoint problematic. Tests 1 and 2 clearly showed (Fig. 2) that four- to five-day-old nestlings do not thermoregulate nearly as well as older nestlings. Body temperature control is much improved by two weeks of age, yet time-lapse films of nests show that some nestlings continue to be brooded by their parents during the third week of growth, especially overnight (Kirkley 1982). Therefore, we concur with O'Connor's (1984) statement that in some cases "the extent of parental brooding is probably the best available guide to the thermoregulatory abilities of the young" under the prevailing conditions.

Nestling behavioral strategies for coping with cold appear to change with nestling age. Hawk nestlings that are too young to thermoregulate effectively tend to vocalize and struggle, which presumably would increase their chances of locating and huddling with siblings or of eliciting parental brooding behavior. Nestlings more capable of shivering thermogenesis tend to lie motionless with the extremities held close to the body, thus conserving heat. Similar age-related changes in the behavior of cold-stressed nestlings have been observed in other species such as Willow Ptarmigan (*Lagopus lagopus*) (Aulie 1976). We observed with time-lapse films and visits to nests that young hawks often huddled together in the nest depression during adult absences, especially when ambient temperatures were low. Dunn (1976, 1979) emphasized the advantage of this means of heat conservation by showing that larger broods of altricial nestlings attain "effective" endothermy at an earlier age than do smaller broods and at a considerably earlier age than predicted from the "physiological" age of endothermy in isolated nestlings.

Tolerance to hyperthermia.—Overheating in avian young is probably more prevalent among species that build nests exposed to direct insolation in hot, arid climates, but hyperthermia can also occur in protected nests such as cavities occupied by many nestlings (Mertens 1977). Beecham and Kochert (1975) report that heat prostration possibly caused 41 percent of the nestling mortality in Golden Eagles (*Aquila chrysaetos*) in southwestern Idaho. Mosher and White (1976) suggest that Golden Eagles may preferentially select nest sites which minimize thermally stressful conditions, a conclusion questioned by Collopy (1980).

Strategies for coping with heat stress involve both behavioral and physiological mechanisms. The restless movements of nestlings of all ages shortly after the illumination of the light panel (Test 3) may have helped them find a place with better convection. In the wild, these movements may also help nestlings locate shaded places on the nest surface or may stimulate a parent to begin shading. When adults and shade are absent, heat-stressed nestlings often climb out onto the nest margin; the slightly elevated position and loose arrangement of the sticks presumably facilitate nestling heat loss through convection. The spread posture of nestlings during heat stress also enhances heat dissipation by exposing the unfeathered areas beneath the wings and on the feet and tarsi. Feet and legs are reported to be important heat dissipating structures in raptors (Bartholomew and Cade 1957, Mosher and White 1978) and in other birds (Howell and Bartholomew 1961, 1962; Kahl 1963; Bartholomew 1966). The importance of the legs in thermoregulation may account for tarsal length as one of the more important predictors of thermoregulatory performance in Test 3.

Panting (or gular flutter in some species) increases the rate of evapo-

rative water loss from the respiratory surfaces and is a primary mechanism for augmenting heat loss in birds (Kirkley 1985). Nestlings in Test 3 began to breathe with their mouths open before their body temperatures had risen more than 1 or 2°C. By the end of 20 min, average breathing rates were 3–5 times that of normal. During panting the beak is opened fully, the tongue is lifted forward from the lower mandible, and the surfaces of the mouth are kept moist with mucus which occasionally drips from the tongue and lower mandible. The tendency in Test 3 for T_b to increase slightly in nestlings of all ages suggests that heat-stressed hawk nestlings may, like other birds (O'Connor 1984), employ adaptive hyperthermia rather than maintaining a normal T_b.

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